

# THE MYRICACEAE OF THE UNITED STATES AND CANADA: GENERA, SUBGENERA, AND SERIES

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## ABSTRACT

The compelling case for recognizing three genera of North American Myricaceae (*Comptonia*, *Morella*, and *Myrica*) is presented. Keys and descriptions are provided for the recognized supraspecific taxa. The nomenclatural basis of each of these genera, subgenera, and series is outlined and discussed if at all controversial. *Morella* Lour., the largest genus, is here treated as comprising two subgenera of which subg. *Cerothamnus* (Tidestr.) Wilbur is found in the Americas and Africa and subg. *Morella* is restricted to eastern and southeastern Asia. There are at least four species of *Morella* in the United States and Canada and perhaps as many as six: *M. cerifera* (L.) Small, *M. caroliniensis* (Mill.) Small, *M. inodora* (W. Bartram) Small, and *M. californica* (Cham. & Schltld.) Wilbur. Those about which there is some question do not have binomials in the genus *Morella* but are known as *Myrica pensylvanica* Mirbel (= *Cerothamnus pensylvanicus* (Mirbel) Moldenke) and *Myrica pusilla* Raf. (= *Cerothamnus pusilla* (Raf.) Small). *Myrica* L. is represented by the circumboreal *M. gale* L. and the Californian *M. hartwegii* S. Watson. *Comptonia* L'Hér. ex Aiton with its only species, *C. peregrina* (L.) J.M. Coulter, is restricted largely to the northeastern United States and adjacent Canada. New combinations and/or rankings are provided for the following taxa: *Morella* subg. *Cerothamnus* (Tidestr.) Wilbur and series *Faya* (Webb & Berthel.) Wilbur, *Morella californica* (Cham. & Schltld.) Wilbur, and for the Azorean *M. faya* (Aiton) Wilbur.

## RESUMEN

Se presenta un estudio convincente para reconocer tres géneros de *Myricaceae* de Norte América (*Comptonia*, *Morella*, y *Myrica*). Se ofrecen claves y descripciones de los taxa supraspecíficos reconocidos. Se bosqueja y discute la base nomenclatural de todos los géneros, subgéneros y series, aunque sea controvertida. *Morella* Lour., el género más amplio, se trata aquí dividido en dos subgéneros de los cuales *Cerothamnus* (Tidestr.) Wilbur se encuentra tanto en América del Norte como del Sur y en Africa, y *Morella* que está restringido al este y sureste de Asia. Hay al menos cuatro especies de *Morella* en los Estados Unidos y Canadá, que quizás puedan llegar a seis: *M. cerifera* (L.) Small, *M. caroliniensis* (Mill.) Small, *M. inodora* (W. Bartam) Small, y *M. californica* (Cham. & Schltld.) Wilbur. Las especies sobre las que hay dudas, no tienen ningún binomen en el género *Morella*, pero se conocen como *Myrica pensylvanica* Mirbel (= *Cerothamnus pensylvanicus* (Mirbel) Moldenke) y *Myrica pusilla* Raf. (= *Cerothamnus pusilla* (Raf.) Small). *Myrica* L. está representado por *M. gale* L., circumboreal, y *M. hartwegii* S. Watson, de California. *Comptonia* L'Hér. ex Aiton con su única especie *C. peregrina* (L.) J. M. Coulter está restringida al noreste de los Estados Unidos y zonas adyacentes de Canadá. Se dan nuevas combinaciones y/o rangos para los siguientes taxa: *Morella* subgen. *Certhamnus* (Tidestr.) Wilbur y serie *Faya* (Webb & Berthel.) Wilbur, *Morella californica* (Cham. & Schltld.) Wilbur y para *M. faya* (Aiton) Wilbur, de las Isla Azores.



For one whose formative years were spent in a section of the country where Small's (1933) *Manual of the southeastern Flora* was the basic reference, numerous adjustments had to be made to relate to the prevailing, more conservative generic concept then dominating most of American botany. Small's "microgenera" were viewed as a provincial aberration. For one's work to be understood by most of the botanical community, one had to convert the generic names employed by Small and other prolific practitioners of the so-called "New York School" such as Britton, Rydberg, and Barnhart into the broader generic concepts employed by more conservative botanists. For example, how many of us know which common genera are intended when one encounters such generic names as *Wallia*, *Cerothamnus*, *Tulipastrum*, or *Phenianthus*? Brandegee (1901) argued vehemently against the generic splitting characteristic of the New York Botanical Garden under the leadership of Nathaniel Lord Britton. She suggested that genera should be so broadly delineated that all reasonably bright 10 year olds could be expected to know the principal genera of plants and animals in their neighborhood. Clearly Brandegee would be disappointed today for not only would most school boys and girls fail her test but so would most university biology professors. In fact, in the past 2 decades the pendulum has swung back strongly towards the generic standards of Britton, Rydberg, and Small. Who could have predicted 2 or 3 decades ago that the well-known genus *Cassia* would disappear from the flora of the Carolinas and be replaced by the segregates *Chamaecrista* and *Senna*; or that *Psoralea* would be confined to southern Africa and that those generic names that Rydberg and Small were castigated for using instead (*Orbexilum*, *Pedimelum*, and *Rhytidomene*) would now be very widely adopted for different elements formerly included in *Psoralea* s.l.?

Turning to Myricaceae, we find that Small (1933) recognized three genera in the area of the southeastern United States: *Myrica* L. (1753), *Comptonia* L'Hér. ex Aiton (1789) and *Cerothamnus* Tidestr. (1910). Radford et al. (1968) also recognized three myricaceous genera in the Carolinas, differing however in the generic names accepted and the groups to which the names applied: *Gale* Adans. (1763), *Comptonia* L'Hér. ex Aiton (1789), and *Myrica* L. (1753). More conservative treatments of Myricaceae recognize, in addition to the controversial and relatively little-known, monotypic, New Caledonian *Canacomyrica* Guillaumin, two genera sometimes combined as subgenera or sections within the broad concept of *Myrica*. Under such a conservative scheme, the genus *Myrica* would consist of three major taxa of very unequal size. The New Caledonian *Canacomyrica* will not be considered in this paper, but it should be noted that considerable doubt has been expressed as to its relationship with Myricaceae (Thorne 1973). The nomenclature of the three North American myricaceous genera is in part controversial as is discussed below.



The morphological evidence summarized in Table 1 argues strongly that there are at least three major groups within non New Caledonian Myricaceae. These three groupings are so fundamentally different that, in my opinion, generic rank should be accorded to each of them. With flowers as greatly reduced as those of Myricaceae, it is not surprising that the most striking differences are found elsewhere—especially in characteristics of fruit and vegetative features. These same groups were treated as three subgenera of *Myrica* by Engler (1894). Gleason (1952) and Gleason & Cronquist (1963) treated all species as *Myrica* with no indication given of infrageneric, supra-specific classification. Many authors including Rehder (1949), Fernald (1950), Hutchinson (1964-), Elias (1971), and Gleason & Cronquist (1991) in the past 5 decades have recognized two genera: *Comptonia* and *Myrica* (sometimes the latter with the two commonly accepted subgenera, *Gale* and *Morella*). Among previous authors recognizing three genera are Chevalier (1901), Rendle (1903), Small (1933), Radford et al. (1968), and Baird (1968).

That there are three major groupings within Myricaceae seems generally agreed upon by most students of the family; the only question is the rank or ranks to be accorded to these seemingly natural, monophyletic taxa. Perhaps a comparable case is *Quercus*, since that genus is traditionally divided into three subgenera by most botanists although Schwarz (1936) treated the subgenera as genera and Oersted (1867) had originally treated those Asian species with connate cupular scales forming concentric rings as the genus *Cyclobalanopsis*. A table or chart comparing the differences between these three fagaceous taxa is both lengthy and impressive, but evaluation of the differences suggests that they are variations on the same theme as opposed to rather dramatic innovations and new themes expressed in the phyletic development of the three lines of Myricaceae.

Although in Table 2 Baird has been outvoted 3 to 1, the preponderance of evidence suggests that he was nomenclaturally correct in the names he employed and the groups to which he applied the names. Small (1903) recognized both *Comptonia* and *Morella* in the southeastern United States but was unaware of the presence of *Myrica gale* there. It is unfortunate that Baird's detailed investigation was never published. I here acknowledge my indebtedness to Baird (1968) for information summarized in his unpublished dissertation that strengthened the case made for the recognition of three genera. It must be admitted that in such matters one can not be dogmatic for the state of our science does not totally exclude individual taste. As long as the groups recognized are seemingly monophyletic (in the pre-cladistical sense) and perhaps reasonably equivalent in morphological differentiation, whether such groups are treated as three genera or three sections or subgenera of one genus is a matter of individual taste doubtlessly tempered by both tradition and the prevailing philosophy of the period.



TABLE 1. Comparing the three genera of the Myricaceae.

	MORELLA	MYRICA	COMPTONIA
Terminal buds	Present	Lacking	Lacking
Leaves	Thick, usually persistent, entire, toothed, or rarely incised	Thin, deciduous, entire or weakly serrate distally	Thin, deciduous, roundedly pinnatifid
Stipules	Lacking	Lacking	Present
Aments	Inserted on old wood mainly below the leaves	Inserted at the summit of the branchlets of preceding year	Inserted in the axils on deciduous branchlets
Stamen number	3-22	Usually 4 but ranging from 3-6 (-9)	Usually 4 but ranging from 3-7
Ovary	Covered with waxy or fleshy emergences; bracteoles none or, if present, non-adnate	Smooth, flanked by 2 entire bracteoles which develop in fruit into wings, strongly adnate	Smooth, flanked by 2 lacinate bracteoles emerging from the base and developing into a loose cupule
Fruits	In very loose clusters; spherical to subspherical nutlet covered by wax-secreting papillae	In dense, subcylindrical spikes; flattened, keeled nutlet made buoyant by two adnate, enlarged and inflated bracteoles	In spherical spikes; conic to cylindrical nutlet enveloped by the elongating and persistent bracteoles and scales forming a bur-like fruiting structure
Adnation of bracteoles with fruit wall	None	Strongly adnate	None
Ectocarp:			
Relative thickness	Thick	Thin	Thin
Cell type	Parenchyma	Parenchyma	Sclerenchyma
Papillae presence	Present	Absent	Absent
Trichomes presence	Absent to dense	Absent	Absent
Surface	Non-sclerified, waxy	Neither hard nor waxy	Sclerified and not enveloped by wax
Cell type of mesocarp	Sclerenchyma	Parenchyma	Parenchyma
Wood	Diffuse porous	Ring porous	Diffuse porous
Chromosome number	n=8	n=24, 48	n=16



TABLE 2.

CHEVALIER (1901)	RENDLE (1903)	RADFORD ET AL. (1968)	BAIRD (1968)
Myrica	Myrica	Myrica	Morella
Gale	Gale	Gale	Myrica
Comptonia	Comptonia	Comptonia	Comptonia

In recognizing genera, botanists would perhaps find that by placing greater emphasis on the currently minimized morphological adaptations between plants and their environment, the disparity between botanical and zoological practice would be less striking than now is the case. The importance of the genus as an indicator of discrete evolutionary lines would be enhanced if the obvious correlation between functional morphology and broadly conceived environmental integration were emphasized (Inger 1958). In the case of Myricaceae, it should be pointed out that these morphological adaptations to differing means of fruit dispersal have not been ignored by botanists even if they have not emphasized the functional role. These characteristics of the fruit have been recognized by even the most conservative botanists in their formal classification but usually at the subgeneric level. My account merely advocates recognition at the generic level.

A principal reason for the widely divergent generic treatments of Myricaceae is not because of differences in interpretations of biological or morphological facts or even in the weight given to these facts; it is simply a disagreement as to the lectotypification of the generic name *Myrica* L. Chevalier (1901), Rendle (1903), and Radford et al. (1968) in effect all treated *Myrica cerifera* L. as the lectotype of the generic name *Myrica*; Baird (1968) accepted *Myrica gale* L. as the lectotype. This confusion exists whether we accept one genus with three equivalently ranked subgroups or recognize three independent genera, but the differences are obviously much more dramatic under the binomial system of nomenclature if three genera are recognized rather than one genus.

Unfortunately the International Code of Botanical Nomenclature (ICBN 1988) still provides remarkably little guidance in the matter of choosing a lectotype. In the absence of clear directions from ICBN, botanists will of necessity flounder along with their divergent conclusions as to what the lectotype of such Linnean genera as *Myrica* should be. A special Committee on Lectotypification was established by the Nomenclature Section of the Sydney Congress to resolve problems such as those pointed out by Stirton et al. (1981). This Committee recommended to the Berlin Congress that Art. 8.1 be amended to read "The author who, on or after 1 January 1935, first designates a lectotype or a neotype must be followed. ..." It was hoped that this stipulation would eliminate the uncertainty connected with use of the term "type" by such early authors as Rafinesque whose concept of type surely was



different than that of a present-day investigator and also the uncertainty of the lectotypes designated under both the American Code and the Type Basis Code. Under this suggested requirement, the genus *Myrica* would have been typified by *M. gale* as that was the choice of Hitchcock and Green and published as an unofficial supplement to the ICBN (1935, p. 116). However, the International Botanical Congress meeting in Berlin in 1988 found itself unable to resolve the problems of lectotypification and, since one committee failed to solve the problem to everyone's satisfaction, three committees were appointed to study and to report their recommendations to the 1993 Congress (Tokyo). As might be expected the complicated problems of lectotypification have been largely passed on to the next Congress.

Both *Myrica gale* and *M. cerifera* have been designated as the lectotype for the generic name *Myrica*. The species best known to Linnaeus as the only member of the genus occurring in Sweden, where it is abundant, is *Myrica gale*. Britton, operating under the American Code, designated this species as the type (= lectotype) of the genus. Hitchcock & Green (1929) made the same choice; their conclusions as to the "standard species" (= lectotype) were listed in the International Rules (1935) in a semi-official way. However, the desirability of *Myrica gale* as a lectotype was challenged by Hylander (1945) since that species with a very few close allies had been segregated as a small, independent genus. If the much larger clade, represented by *Myrica cerifera*, were to be segregated from *Myrica* this larger portion of the genus, a group of ca. 50 species, would belong to this segregate almost all requiring new combinations. Rehder (1949) also accepted *Myrica cerifera* as the lectotype of the genus *Myrica*. In spite of this consideration, it seems certain that *Myrica gale*, the historically best or at least the scientifically longest known species of *Myrica*, will be confirmed as the lectotype of the genus. Preliminary reports of the subcommittee dealing with lectotypification of Linnaean generic names strongly suggest that *Myrica gale* will be recognized as the lectotype of *Myrica* L.

#### KEY TO THE AMERICAN GENERA OF MYRICACEAE

1. Terminal buds present; distal axillary buds vegetative; mature fruit both papillose and wax-covered; anthers forming in the spring shortly prior to flowering; fruit a spherical or subspherical nutlet covered by wax-secreting papillae ..... 1. *Morella*
1. Terminal buds absent; distal axillary buds floral; mature fruit lacking papillae, somewhat resinous but never bearing a waxy coating; anthers formed in the fall preceding flowering; fruit either flattened and keeled or conical to cylindrical, neither wax-coated nor papillate.
  2. Leaves stipulate; leaf margin entire or serrate; bracteoles of pistillate flowers 2, unlobed, adnate to the fruit; fruit a flattened, keeled nutlet rendered buoyant by the two adnate, enlarged, unlobed inflated bracteoles ..... 2. *Myrica*



2. Leaves stipulate; leaf margins deeply pinnatifid with broadly rounded lobes; bracteoles of pistillate flowers 2, deeply lobed into linear segments, not adnate to the conic to cylindric fruit; fruit a conic to cylindric nutlet enveloped at maturity in a bur-like involucre formed from the lobed bracteoles and the accompanying bracteal scale ..... 3. *Comptonia*

1. *MORELLA* Lour.

**Morella** Lour., Fl. Cochinch. 548. 1790. TYPE: *Morella rubra* Lour.

KEY TO THE SUBGENERA OF *MORELLA*

1. Aments branched; pistillate bracts subtending several ovaries of which only one develops; fruit 6–8 mm in diameter, covered at maturity by imbricate, fleshy, succulent papillae ..... subg. 1. *Morella*  
 1. Aments simple; pistillate bracts usually solitary, simple, and 1-flowered; fruit 1–5 mm in diameter, covered at maturity usually by wax-secreting, neither fleshy nor succulent papillae ..... subg. 2. *Cerothamnus*

*MORELLA* subgenus *MORELLA*

**Morella** Lour., Fl. Cochinch. 548. 1790. TYPE: *Morella rubra* Lour. *Myrica* sect. *Morella* (Lour.) Benth. & Hook.f., Gen. Pl. 3:401. 1880. *Myrica* subg. *Morella* (Lour.) Engler, Nat. Pflanzenfam. II. 1:27. 1893.

Subgenus *Morella* apparently contains fewer than 10 species of eastern Asia, the Philippines, and Malaysia. The differences between the species of subg. *Morella* and subg. *Cerothamnus* from both the Americas and central and southern Africa are so striking as to have elicited expressions of consternation from Greene (1910) that Small (1903) would transfer our southeastern species to *Morella*; this dismay was shared by Nieuwland (1910). Greene could not believe that plants whose fruits were so palatable and wholesome as to be eaten both uncooked and cooked and so succulent and juicy as to be made into a flavorful wine could belong to the same genus as the hard, waxy-fruited plants of the southeastern United States or the western coastal region from Vancouver Island throughout much of California. Perhaps Greene was correct in his assessment, but for the present, based largely upon the findings but not the conclusions of MacDonald (1978) and Abbe (1972), the Asiatic plants are here treated as merely subgenerically differentiated from their American and African congeners.

**Morella** Subgenus *Cerothamnus* (Tidestr.) Wilbur, comb. & stat. nov.

*Cerothamnus* Tidestr., Elys. Marian., Ferns. 41. 1910. LECTOTYPE: *Cerothamnus arborescens* (Castigl.) Tidestr. (= *Myrica cerifera* L.) [herein designated].

Usually aromatic, dioecious or polygamo-monoecious shrubs to small trees with terminal buds. Leaves alternate, pinnately veined, deciduous or evergreen, entire or serrate, estipulate. Inflorescences borne proximally below or axillary to the lower leaves, the staminate erect or nearly so, at anthesis



thick-cylindric to broadly ellipsoid, bracts broadly to narrowly ovate and at anthesis shorter than the 1–22 stamens, the stamens yellow or becoming yellow, filaments simple or branching and arising from the staminal column at different levels, the secondary, tertiary and even quarternary bracts often present; pistillate inflorescences simple or basally branched, at anthesis ovoid to cylindrical, the rachis sometimes glandular and the bracts usually persistent, the pistillate flower subtended by secondary, tertiary, or even quarternary bracts forming a calyculus, the ovary either glabrous or pilose and almost completely covered by persistent, more or less globular, wax-secreting papillae. Fruit a nutlet,  $\pm$  spherical and mostly covered by a layer of wax, the ovary wall glabrous to densely pilose, the papillae glabrous to puberulent, the associated secondary, tertiary, and even quarternary bracts, if all present, persisting until after fruit maturation and never enlarging.

*Cerothamnus*, the largest subgenus in Myricaceae, contains the waxy-fruited species of *Morella* native to the Americas and Africa and their neighboring islands—i.e. the West Indies and the Atlantic islands lying off the northwestern coast of Africa.

#### KEY TO THE SERIES OF SUBGENUS *CEROTHAMNUS*

1. Staminate flowers with 3–7 stamens; staminal column branches each with only 1 anther; bracteoles 0–3; pistils solitary in axil of a bract; fruit wall glabrous or, if pubescent, then the papillae also pubescent ..... Ser. 1. *Cerothamnus*
1. Staminate flowers with (6-)8–18(-22) stamens; staminal column branches often with 2 anthers; bracteoles 2–6; pistils 1–3 in axil of each bract; fruit wall but not the papillae densely pubescent ..... Ser. 2. *Faya*

#### **Morella series *Cerothamnus* (Tidestr.) Wilbur, comb. & stat. nov.**

*Cerophora* subg. *Cerocarpa* Raf., Alsogr. Amer. 11. 1838. LECTOTYPE: *Cerophora lanceolata* Raf., herein designated [= *Myrica cerifera* L.]

*Myrica* sect. *Cerophora* (Raf.) A. Chev., Mém. Soc. Sci. Nat. Cherbourg 32:223 (= Monogr. Myric. p.139) 1901.

*Cerothamnus* Tidestr., Elys. Marian., Ferns. 41. 1910. LECTOTYPE: *Cerothamnus arborescens* (Castigl.) Tidestrom (= *Myrica cerifera* L.)

Aments simple; pistillate usually solitary, simple, and 1-flowered. Fruit 1–5 mm in diameter. Papillae wax-producing, neither juicily succulent nor fleshy.

In spite of the few species in *Morella* series *Cerothamnus* present in eastern North America, there currently exists a surprising amount of uncertainty as to just how few or how many species can be recognized in that well-collected area. The number of species are in any event few: perhaps no more than two and certainly no more than four.

1. ***Morella cerifera* (L.) Small, Fl. SE U.S. 337 & 1329. 1903. *Myrica cerifera* L., Sp. Pl. 1024. 1753. *Cerothamnus ceriferus* (L.) Small, Fl. Miami 61 & 200. (26 Apr) 1913.**



2. A second taxon has been proposed whose distinctness from *Morella cerifera* is denied by several of our more experienced students of the southeastern flora. The questioned taxon is usually a low bushy, rhizomatose plant with strikingly smaller leaves. It was treated by Michaux (1803) and Radford et al. (1968) as a variety (*Myrica cerifera* var. *pumila* Michx.) but as a species by Rafinesque (1838) and Small (1903 and 1933) (*Myrica pusilla* Raf., *Morella pumila* (Michx.) Small, and *Cerothamnus pumilus* (Michx.) Small).

Many field observers and collectors of bayberries, are at least partly convinced that *Myrica pusilla* merits taxonomic recognition for these dwarf plants seem strikingly unlike the much more abundant and luxuriant *M. cerifera* that often grow in close proximity. In the herbarium on the other hand the claim to specific or even varietal status of *M. pusilla* seems much less certain perhaps because most specimens are not accompanied by notes as to either the height or habit of the plant; those two features together with the much smaller size of the leaves are what makes these plants in the field so strikingly unlike the ubiquitous *M. cerifera*. In spite of the apparent distinctiveness noted in the field, it seems impossible to maintain as distinct *cerifera* and *pusilla* even in a group as plastic or as bereft of taxonomically useful characters as are the bayberries. Sufficient dissatisfaction with this conclusion exists, however, that I intend and would urge all other botanists with the opportunity to study and collect the plants in the field to do so and to record carefully notes on the height, habit and habitat of the plants—something that surprising has been largely neglected by most collectors even in recent decades.

Thieret (1966), who has had extensive field experience with both species in Louisiana, noted that “from a clump that is otherwise typically *M. pusilla*, there will arise one main stem to ten or twelve feet tall and six inches in diameter—a *M. cerifera* stem. Examination reveals that all the stems of the clump comprise a clone. . . . Plants intermediate in habitat between the two extremes are usually found in the vicinity.” Thieret concluded that “the habit differences . . . are not reliable criteria but are simply responses to habitat differences” and “that the habit extremes pass insensibly into each other.” I too have often observed in North Carolina both *pusilla* and *cerifera* growing in close proximity but have not yet noted the blurring of growth form and leaf size that Thieret has noted nor am I convinced that there is always a correlation of habitat and growth form. I have regrettably never tried to excavate the underground connection perhaps implied by Thieret and which, if proven, would provide convincing support for the treatment tentatively accepted here of non-recognition (unless root grafting occurred). Godfrey (1988), whose field experience with our southeastern plants is



surely unrivalled, does not accept the dwarf plants as a taxon deserving a name either. Additional study is certainly needed, especially investigations centered in the field.

3. **Morella caroliniensis** (Mill.) Small, Fl. SE U.S. 337 & 1329. 1903 [as *Carolinensis*]. *Certhamnus caroliniensis* (Mill.) Tidestr., Elys. Marian., Ferns. 41. 1910.

*Myrica heterophylla* Raf., Alsogr. Amer. 9. 1838 [as "heterophylla"]: TYPE LOCALITY: "Carolina to Florida." *Certhamnus heterophylla* (Raf.) Moldenke, Phytologia 29:386. 1975.

4. **Myrica pensylvanica** Mirbel, Traité Arbr. Arbust. 2:190. 1804, [not Loisel. as usually cited!]. *Certhamnus pensylvanicus* (Mirbel) Moldenke, Rev. Sudam. Bot. 4:16. 1937.

Although my study is not completed, I am doubtful that the above two species can be maintained as distinct. The alleged principal difference between the two is apparently to be found in the fruits: fruit of more northern species (*Myrica pensylvanica*) possess puberulence on both the papillae and ovary wall; fruit of the southern species (usually referred to as *Myrica heterophylla* Raf.) have glabrous papillae and glabrous walls. Due to the dense covering of wax, detection of the puberulence is often difficult and the amount varies from a dense covering to very few trichomes. The other alleged differences of fruit size, twig pubescence, leaf persistence, etc. seem even less consistently diagnostic. If only one species is to be recognized, the correct binomial is *Morella caroliniensis* (Mill.) Small, a binomial that has been applied to the combined species in the past and to both of the species at different times when they were treated as distinct species. Miller's name should be applied to the species with the more southern distribution if two species are represented as most authors have accepted for the past 75 years.

5. **Morella inodora** (W. Bartram) Small, Fl. SE U.S. 337 & 1329. 1903. *Myrica inodora* W. Bartram, Travels Carolina, 405. 1791. *Certhamnus inodorus* (W. Bartram) Small, Florida Trees 12 & 102. 1913.

In striking contrast to most other Myricaceae, but as indicated by its specific epithet, the crushed foliage of *Morella inodora* is not aromatic. The species ranges from southern Georgia westward into southeastern Louisiana.

6. **Morella californica** (Cham. & Schltld.) Wilbur, comb. nov. *Myrica californica* Cham. & Schltld., Linnaea 6:535. 1835. *Gale californica* (Cham. & Schltld.) Greene, Man. Bot. San Francisco. 298. 1894.

The natural range of this species apparently extends from central coastal Washington south into Los Angeles County, California at elevation of 150 m or less.



**MORELLA** series **FAYA** (P. Webb & Berthel.) Wilbur, comb. & stat. nov.

*Fayana* Raf., Alsogr. Amer. 12. 1838. TYPE: *Fayana azorica* Raf. (= *Myrica faya* Aiton).

*Faya* P. Webb & Berthel., Hist. Nat. Iles Canaries 3:272, t. 216. 1847. TYPE: *Faya fragifera* P. Webb & Berthel. (= *Myrica faya* Aiton). *Myrica* sect. *Faya* (P. Webb & Berthel.) C. DC., Prodr. 16(2):151. 1864.

Aments simple or branched; pistillate bracts subtending several ovaries of which only some usually develop. Fruits usually 4–6 mm in diameter, often forming a syncarpium. Papillae often producing wax but never fleshy.

Series *Faya* is a small taxon of three geographically widely separated species. Besides the two North American representatives treated below, the section is composed of the type species of the section, *Morella faya*<sup>1</sup> of the Canaries, Madeira, and the Azores and possibly also of Portugal where it occurs but perhaps only as a naturalized introduction Burges (1964). MacDonald (1977, p. 2638), who has presented a series of papers on the morphology of the inflorescence of many myricaceous taxa, is of the opinion that “section *Faya* could easily be incorporated in section *Cerophora*” of the genus *Myrica*. This genus in his opinion would then consist of the fleshy-fruited section *Morella* of eastern Asia and Indonesia and section *Cerophora*, the largest taxon in the family, with both American and southern African representatives. The suspicion lingers that series *Faya* is not a proven monophyletic group not only because MacDonald questioned its morphological distinctiveness but also because its distribution pattern is not one readily explained or matched by other examples.

In contrast to the uncertainty existing in both the identities and names of the taxa comprising *Morella* series *Cerothamnus*, the taxa forming series *Faya* are morphologically most distinct and geographically widely separated.

## 2. MYRICA L.

**Myrica** L., Sp. Pl. 1024. 1753; Gen. Pl. ed. 5.449. 1754. LECTOTYPE: *Myrica gale* L.

*Gale* Dumort., Fl. Belg. 12. 1827. [Neither *Gale* Duhamel, (Traité Arbr. Arbust. 1:253. 1755) nor *Gale* Adanson., (Fam. Pl. 1763.) Both Duhamel’s and Adanson’s reintroduction of *Gale* were illegitimate names as substitutions for *Myrica* L. and hence nomenclaturally superfluous (Art. 63 ICBN)].

*Myrica* “b” *Gale* [Tourn.] Endl., Gen. Pl. 272.1837. [Employed in the sense of the Myricaceae less *Comptonia*.]

*Cerophora* subg. *Galestis* Raf., Alsogr. Amer. 11. 1838. LECTOTYPE: *Cerophora (Galestis) angustifolia* Raf. (= *Myrica gale* L.)

*Angeia* Tidestr., Elys. Marian., Ferns 37. 1910. TYPE: *Angeia palustris* (Lam.) Tidestr. (= *Myrica palustris* Lam., = *Myrica gale* L.)

<sup>1</sup>*Morella faya* (Aiton) Wilbur, comb. nov. BASIONYM: *Myrica faya* Aiton, Hort. Kew. 3:397. 1789.



Aromatic, usually dioecious shrubs lacking terminal buds. Leaves alternate, pinnately veined, serrate to entire, deciduous, estipulate. Inflorescences borne distally, the staminate suberect to recurved, in bud ovoid to elliptical and at anthesis cylindrical, the bracts broadly ovate to triangular, at anthesis longer than the 3–6 stamens, secondary bracts absent; pistillate inflorescences simple, broadly cylindrical at anthesis, the bracts persistent, the pistillate flowers each subtended by 2 secondary bracts partially adnate to the ovary wall, the ovary glabrous and lacking papillae. Nutlet flattened, keeled, not covered with wax but with few to many glandular trichomes, the bracteoles persistent, becoming greatly enlarged and inflated, strongly adherent to the flattened fruit, inflated and forming a buoyant float.

*Myrica* is represented in the Americas by two species that are morphologically readily distinguished from one another and whose geographical ranges do not overlap.

### 1. *Myrica gale* L.

This species has a broken circumboreal distribution pattern extending across Canada and Alaska and south to northern New Jersey, Pennsylvania, eastern Ohio, and about the Great Lakes from as far west as eastern Minnesota and in the west to the mountains of Oregon. Morphological variation apparently correlated with distribution occurs within the extensive range of this species but its taxonomic merit requires additional study. Hultén (1944 and 1968) presented a brief overview of the problem.

### 2. *Myrica hartwegii* S. Watson.

This species is found along stream banks in yellow pine forests in the Californian Sierra between 300–1500 m and consequently not sharing any part of its range with any other member of the Myricaceae.

### 3. COMPTONIA L'Hér. ex Aiton

**Comptonia** L'Hér. ex Aiton, Hort. Kew. 3:334. 1789. TYPE: *Comptonia asplenifolia* (L.) L'Hér. ex Aiton (= *Comptonia peregrina* (L.) J.M. Coulter).

*Myrica* "c" *Comptonia* (L'Hér. ex Aiton) Endl., Gen. Pl. 272. 1837.

*Myrica* sect. *Comptonia* (L'Hér. ex Aiton) Endl. ex C.DC., Prodr. 16(2):151. 1864.

*Myrica* subg. *Comptonia* (L'Hér. ex Aiton) Engler, Nat. Pflanzenfam. III. 1:28. 1893.

Aromatic, usually dioecious, colonial shrubs 1.5 m tall or less and lacking terminal buds. Leaves alternate, pinnately veined and lobed, deciduous, conspicuously semi-cordately stipulate. Inflorescences borne distally, the staminate suberect to strongly recurved, cylindrical, the primary bracts persistent, broadly ovate to quadrangular, at anthesis longer than the 3–7 stamens, adaxially bearing numerous glandular trichomes, secondary bracts



absent; pistillate inflorescences simple, broadly ovoid at anthesis, the rachis pubescent and glandular, the bracts persistent but in fruit obscured by the greatly enlarged lobes of the secondary bracts, the pistillate flower subtended by the 2 greatly enlarged and deeply lobed secondary bracts, the ovary glabrous and lacking papillae. Nutlet conical to cylindrical, non-ceriferous, 2.2–5.5 mm long, glabrous, surrounded by the enlarged lobes of the secondary bracts, which form a bur-like structure in fruit.

The genus *Comptonia* is both monotypic and endemic to eastern North America.

1. *Comptonia peregrina* (L.) J.M. Coulter, Mem. Torrey Bot. Club 5:127. 1894. *Liquidambar peregrina* L., Sp. Pl. 999. 1753. *Myrica peregrina* (L.) Kuntze, Revis. Gen. Pl. 2: 638. 1891.

*Myrica asplenifolia* L., Sp. Pl. 1024. 1753. *Liquidambar asplenifolia* (L.) C.F. Ludwig, Neuere Wilde Baumz. 27. 1783. *Comptonia asplenifolia* (L.) L'Hér. ex Aiton, Hort. Kew. 3:334. 1789. *Comptonia peregrina* var. *asplenifolia* (L.) Fernald, Rhodora 40:410. 1938.

The variation in vegetative pubescence suggested by Fernald as a diagnostic feature distinguishing var. *peregrina* from var. *asplenifolia* (L.) Fernald does not delimit populations as sharply as Fernald's account implied. There seems to be more continuous variation in pubescence than Fernald reported and the geographic range of the two pubescence types is less discrete than suggested. Well-collected areas of the mid-Atlantic States have many examples of both pubescence types within their borders. Examples of different pubescence types on different branches of the same shrub are not unusual. It surely can be concluded that varietal status within the monotypic genus *Comptonia* based on pubescence has not been convincingly proven. My rapid survey of hundreds of specimens does not suggest that a detailed, careful analysis of pubescence would likely demonstrate the presence of geographically based varieties.

As shown by the above synonymy, Linnaeus treated this species twice in *Species Plantarum*. The species was first included (p. 999) as *Liquidambar peregrina* and again (p. 1024) as *Myrica asplenifolia*. For nearly a century and a half the name most frequently adopted was *Myrica asplenifolia* or its derivative *Comptonia asplenifolia*. For the past century (except for Gleason (1952), Gleason & Cronquist (1963), and Wagner et al. (1990), the accepted name has been almost universally that based upon *Liquidambar peregrina*. The latter choice is mandated by the International Code not because of the American Code's favoring of the name appearing first in a volume ("page priority") but because Linnaeus, upon discovering the conspecificity of the two binomials, was the first to unite them (Syst. Nat. ed. 10. 2: 1273. 1759.) by placing *Myrica asplenifolia* in the synonym of *Liquidambar peregrina*.



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